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THE AUDITORY REGION OF THE BORHYAENID MARSUPIAL *CLADOSICTIS*

By

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Since the appearance of Sinclair's memoir on the marsupials of the Santa Cruz formation of Patagonia (1906), it has been known that certain members of the Borhyaenidae, such as *Borhyaena* and *Prothylacynus,* were peculiar among marsupials in lacking a tympanic process, or bulla, of the alisphenoid. So far, indeed, had reduction of this bone been carried in *Borhyaena* that all trace of the foramen ovale had disappeared, the mandibular nerve evidently having passed out between alisphenoid and tympanic without so much as a notch to mark its passage. Sinclair was, however, able to show that lack of a tympanic process of the alisphenoid was not characteristic of the family as a whole, this structure being present in at least two genera, *Cladosictis* and *''Amphiproviverra''* (=*Thylacodictis*). His observations have been confirmed by others (e.g. Wood, 1924). Recently, the surprising statement has been made by McDowell (1958, p. 173) that ''the borhyaenines show no clear relationship to other marsupials (they have no alisphenoid bulla, otherwise characteristic of marsupials, for example).'' Even if this claim were correct, these animals would not be unique in this respect within their order. As has long been known (e.g. van Kampen, 1905, pp. 406-407), *Phascolomis* lacks an alisphenoid bulla, although it is remarkable in possessing a process from the squamosal that fulfills the same function.

In the course of a recent visit to Princeton University, I was able once more to examine the borhyaenid material described by Sinclair and reassure myself that his descriptions were correct. In the course of this examination I came across an undescribed specimen that adds to knowledge of the borhyaenid auditory region. This is Princeton University no. 15705, consisting of various fragments, among which is an incomplete cranium. It had been identified, presumably by Sinclair himself, as *Cladosictis lustratus* Ameghino, a determination which there is no reason to doubt. From the fact that Sinclair made no mention of the specimen in his memoir, I suspect that it was not prepared prior to publication. Professor Glenn L. Jepsen very kindly loaned me the cranium for description. The accompanying figures are the work of Mrs. Dorothy Marsh.

DESCRIPTION

The cranium is broken off anteriorly in the vicinity of the postorbital constriction and has been considerably damaged by weathering, which has removed the condyles, the bases of the zygomatic arches together with the glenoid cavities, and much of the bone of the right side. Compensating for these losses is the almost complete lack of crushing, something that cannot be said for the specimens of this species that Sinclair described and figured.

As in other borhyaenines, and unlike the crushed specimen figured by Sinclair (pl. 55, fig. 1), the basisphenoid and basioccipital progressively increase in width posteriorly. As he noted, neither bone has a distinct median keel and both are relatively flat transversely; at the suture they form a fairly prominent transverse ridge. No carotid foramen is to be seen in the basisphenoid; in fact the only foramen visible in this bone is a minute one immediately antero-internal to the foramen ovale. Between basioccipital and periotic there is a conspicuous foramen antero-internal to and almost as large as the foramen lacerum posterius. This is the posterior carotid foramen of Gregory (1910, p. 233); a wide, deep groove in the posterolateral portion of the basioccipital leads forward to it. The significance of this foramen is discussed below. The pars petrosa of the periotic, as is clearly seen on the left side, is rather sharply pointed anteriorly and extends far forward. Except for the opening of the foramen just described, the medial border of the pars petrosa abuts very closely against the basioccipital and basisphenoid.

There is a long and low, slightly curved and narrow auditory bulla that does not project ventrally below the basicranium. The anterior two-thirds of this structure is formed by the alisphenoid. Antero-externally, this portion is suturally united with the squamosal (part of this area is broken away in the specimen). Medially, there is a long, fairly wide and deep depression between the basicranium and the alisphenoid, which is roofed by the pars petrosa. The Eustachian tube opened into the posterior portion of this depression and passed forward within it. On the broken right side of the specimen a natural section of the alisphenoid portion of the bulla is preserved. This is revealed as a deep, oval chamber situated almost entirely within the lateral wall of the cranium. It is separated from the rather large, circular epitympanic recess by a low ridge formed by the alisphenoid anteriorly and the squamosal posteriorly. The remaining third of the bulla is formed by the periotic, which meets the

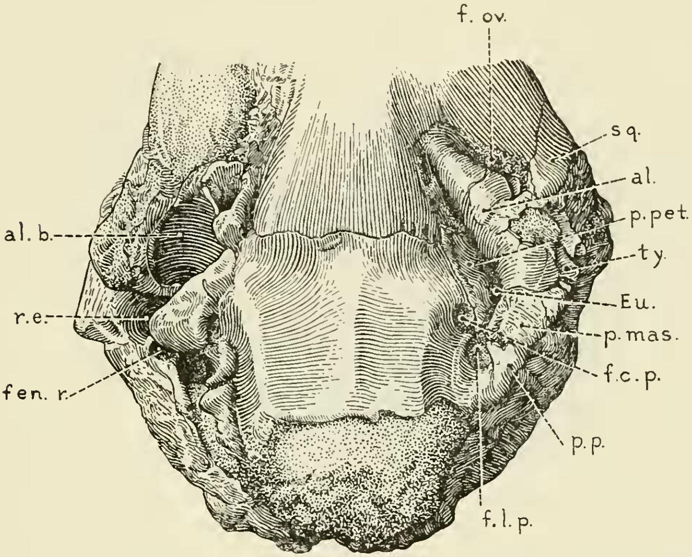

Fig. 1. *Cladosictis lustratus* Ameghino. Ventral view of incomplete cranium. Princeton University no. 15705, X2. Abbreviations: *al.*, alisphenoid; *al. b.*, alisphenoid bulla; *Eu.*, opening for Eustachian tube; *f.c.p.*, posterior carotid foramen; *f.l.p.*, foramen lacerum posterius; *f. ov.*, foramen ovale; *fen. r.*, fenestra rotunda; *p. mas.*, pars mastoidea of periotic; *p. p.*, paroccipital process; *p. pet.*, pars petrosa of periotic; *r. e.*, epitympanic recess; *sq.*, squamosal; *ty.*, tympanic.

alisphenoid in a suture anteriorly and is clasped posteriorly by the heavy, squat and blunt paroccipital process. The portion of the periotic involved is not the pars petrosa, which, as in other borhyaenines, exhibits no trace whatever of a tympanic process, but the pars mastoidea, which, in this form at least, had enlarged downward and forward from the ventro-lateral corner of the occipital surface.

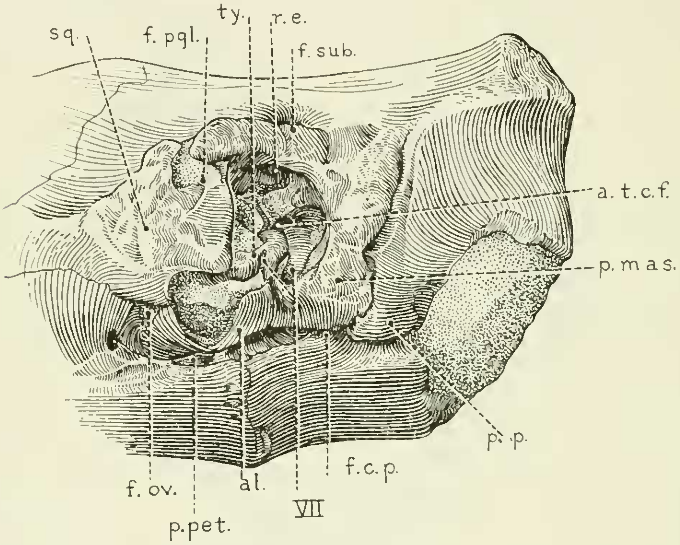

Fig. 2. *Cladosictis lustratus* Ameghino. Lateral and slightly ventral view of incomplete cranium. Princeton University no. 15705, X2. *a.t.c.f.*, apertura tympanici canalis facialis; *f. pgl.*, postglenoid foramen; *f. sub.*, subsquamosal foramen; *VII*, grooves for facial nerve; other abbreviations as in Figure 1.

The meatus — a meatus spurious — is large, very short, and deeper than long; it is bounded anteriorly and dorsally by the squamosal, posteriorly by the squamosal above and the pars mastoidea below (the suture between these bones is unfortunately not distinct), and ventrally by the alisphenoid in front and the pars mastoidea behind. The tympanic is present on the left side. It is free of the bulla and gives the appearance of having been situated wholly or almost wholly within it, although evidently lying close to the bony meatus. The bone has the primitive horseshoe shape so frequently encountered in the order; it is, so far as can be seen, slightly enlarged ventrally, and has a short, dorsally tapering posterior crus. Due to slight forward displacement, the anterior crus is concealed by the squamosal; this displacement is evidence that, as is usual in marsupials, the tympanic was not fused to the skull. The internal surface of the pars mastoidea is grooved anteriorly for the passage of the facial nerve, and there is a corresponding slit in the ventral face of the tympanic.

DISCUSSION

This is the first specimen of a borhyaenine in which a fully formed auditory bulla has been preserved, but it is not unique in the family. A complete bulla, superficially similar to that of the machairodontines, is known in *Thylacosmilus.* In a brief description that I gave of this structure (*in* Riggs, 1934, p. 13), the alisphenoid was identified as a component, although the extent of its participation could not be determined, and the pars mastoidea and paroccipital were recorded as ''overlapping'' the bulla; uncertainty was expressed as to whether or not the tympanic and a tympanic wing of the pars petrosa also participated. With Princeton University no. 15705 in hand I have recently gone over the *Thylacosmilus* material in the Chicago Natural History Museum, hoping for a clearer interpretation in the light of this new evidence. It now seems virtually certain that the tympanic was situated within the bulla, as in *Cladosictis,* but, for the rest, cracks, absence of recognizable sutures and slight distortion prevent any assurance regarding the elements contributing to the posterior portion of the bulla. I am now very dubious as to the existence of a tympanic wing of the pars petrosa and suspect that only the pars mastoidea was involved in the bulla, but certainty on these points can only come with additional evidence.

As has long been known, the borhyaenids show very definite resemblances to two marsupial groups, the Didelphoidea and the Dasyuroidea, and there has been controversy as to whether they were definitely dasyuroid, even thylacinine, or an offshoot from the didelphoid stock. The evidence has been summed up by Simpson (1941), who, in general agreement with such earlier authors as Winge, Ameghino, and Matthew, concluded that while all three groups are clearly related, and very probably had a common ancestry, the Borhyaenidae were descended from the

Didelphoidea, the resemblances between them and the larger members of the Dasyuridae being due to parallelism. With this view I am in complete accord, and the structure of the auditory region contributes a few additional points to its support. In the Dasyuridae there is a large depression or recess in the squamosal, postero-lateral to the small recessus epitympanicus, which is covered by the pars flaccida of the tympanic membrane; no such depression is present in the Didelphidae and Borhyaenidae. The facial nerve in dasyurids, after leaving the middle ear cavity, runs through a bony canal formed mainly by the pars mastoidea with the squamosal contributing antero-ventrally (*Thylacinus,* in which there is only a groove in the pars mastoidea, is an exception); no such canal occurs in didelphids and borhyaenids. Borhyaenids, so far as known, lack a tympanic process of the pars petrosa. In the Didelphidae this process is less developed than in the Dasyuridae, in which it usually contributes largely toward the formation of the bulla (*Thylacinus,* which lacks the process, is again an exception). Two borhyaenine genera are known to lack an alisphenoid bulla. This structure is smaller in a number of didelphids than is the rule among dasyurids. *Cladosictis* is peculiar among marsupials in the participation of the pars mastoidea in the bulla, but it is not unique in this respect. The remarkable little *Dromiciops,* which, with Reig (1955), I believe to be a surviving microbiotheriine didelphid, has a large, complete bulla in which, in addition to a tympanic wing of the pars petrosa, the pars mastoidea is involved posteriorly. Sinclair (p. 410, pl. 62, fig. 7) has figured a specimen of *Microbiotherium* with a fully formed bulla, to which this element may well have contributed, and, as noted above, the same may well have been true of *Thylacosmilus.*

THE INTERNAL CAROTID ARTERY IN THE THERIA

Shortly after preparing this description I had the opportunity to make a field dissection of the head of an opossum (*Didelphis marsupialis*). In the course of this, I noted a small branch leaving the internal carotid artery at the level of the foramen lacerum posterius, passing into the cranial cavity through the posterior carotid foramen and there joining the circle of Willis. The observation was subsequently confirmed in injected specimens by Miss Suzanne Kreinbrook in the Biological Laboratories, Harvard University. This condition is widespread in the Marsupialia, to judge from the nearly universal occurrence of the posterior carotid foramen. Among the Recent genera I have been able to examine, the foramen appears to be lacking only in the microbiotheriines, and in *Acrobates* — and possibly *Phascolarctos* — among the Phalangeridae. Even in these cases it is impossible to be certain short of dissection, for the foramen may be little more than a slit between the basioccipital and the periotic, as in caenolestids, or, apparently, confluent with the foramen lacerum posterius, as in some macropodids.

The internal carotid artery passes through the basisphenoid in pelycosaurs and therapsids (e.g. Romer and Price, 1940; Olson 1944), and also in non-therian mammals so far as known — Monotremata, Triconodonta (Kermack, 1963) and Multituberculata (Simpson, 1937). The marsupials have retained this primitive condition, but have an alternate route in the small branch of the artery that passes through the posterior carotid foramen. *Cladosictis,* so far as I am aware, is the only member of the order in which this alternate route was fully followed, and in which the anterior portion of the artery and the foramen in the basisphenoid was lost. *Cladosictis* had, in fact, essentially and independently achieved the placental condition.

Retention of the primitive condition in marsupials suggests that the placental arrangements were not attained until after the eutherian-metatherian dichotomy, presumably at some time or times during the Cretaceous. Just how these arrangements came about is, of course, unknown. The posterior carotid foramen alternate route may have been followed by all or by some placental groups, but the possibility would appear to exist that a small, more anterior branch may have reached the cranial cavity via an opening antero-internal to the tympanic region (a forerunner of the foramen lacerum medium), and that this eventually became the anterior portion of the internal carotid. In either case the artery would have run forward along the medial edge of the periotic and could thus have readily become enclosed in a groove or canal between basicranial and auditory elements. The stapedial artery presumably came into existence quite early in placental history. Matthew (1909), who recorded its presence in arctocyonids, creodonts and miacids, suggested, rightly I suspect, that the internal carotid early became divided into medial and lateral (stapedial) divisions. With the establishment of these main branches, and given the relative ease with which blood vessel patterns may change, a variety of combinations became possible. Independent acquisitions of similar patterns could have occurred and almost surely did occur. Since the supply of blood rather than the route taken by it is the important thing, it is doubtful if there is any selective advantage in one vessel pattern over another. How varied these patterns may be has recently been demonstrated by Guthrie (1963) for the rodents. Within this one order almost all possible variations are present; in some groups both internal carotid (medial) and stapedial (lateral) branches occur; in others one of these is absent, and in yet others both are wanting.

Details of the carotid circulation appear to be of dubious value as an item of evidence for determining higher affinities within the Eutheria.

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